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Research Article

Could alien *Impatiens capensis* invade habitats of native *I. noli-tangere* in Europe? – Contrasting effects of microhabitat conditions on species growth and reproduction

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Abstract

Recent declines in the population size and habitat of the native European *Impatiens noli-tangere* have led to its observed disappearance. The spread of the North American *I. capensis* in Europe presents a potential additional threat. However, comparative studies on natural populations of the two species are still lacking. Our research aimed to elucidate the determinants of potential habitat segregation between the two *Impatiens* species in the natural environment and to identify key factors influencing variations in their growth and reproduction traits. Fine spatial scale studies allowed for a detailed description of microhabitat conditions and demonstrated the high explanatory power of our multidimensional models. The two species have overlapping environmental distributions, but the range of habitats supporting *I. noli-tangere* is narrower than that of *I. capensis*. The contrasting patterns in species traits result from different responses of each *Impatiens* species to environmental factors. A comparison of RDA results showed the environmental factors to explain 86.4% of the trait variability in *I. noli-tangere*, the soil Pb content (56%) and habitat fertility (21%) being most influential, followed by shading and the soil pH and Ca content. In *I. capensis*, environmental variables accounted for 70.7% of the variability, with shading being the most significant (29%), followed by anthropogenic pressure, aphid presence, soil pH, and moisture content. Our findings suggest no strong habitat barriers preventing *I. capensis* from entering habitats occupied by *I. noli-tangere*. While *I. capensis* invasion in Poland is still in the early stages and no co-occurrence of both species has been reported in European forests, *I. capensis* may eventually colonize forest habitats, given its preference for understory conditions in its native range. The higher sensitivity of *I. noli-tangere* to environmental changes and its weaker performance raise concerns about its ability to persist if *I. capensis* continues to spread.

Key words: Ecological niche, *Impatiens capensis*, *Impatiens noli-tangere*, intraspecific variability, multivariate analysis, soil parameters, species traits

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Introduction

Invasive alien species pose a significant threat to the biological integrity of native ecosystems and local and global biodiversity (Butchart et al. 2010; Simberloff et al. 2013; Doherty et al. 2016; Najberek et al. 2024). The negative effects of the invasion are experienced primarily in the biological sphere, but also in the economic

and social spheres. One huge problem is the impact of invasive alien species on native ones. Blackburn et al. (2019) showed that invasive alien species contributed to the extinction of 25% and 33% of plant and animal species, respectively. Examining the specific traits of plants that contribute to the success in colonization and reproduction of invasive species, such as growth, abundance of flowers, fruit and seed production, is particularly valuable. Moreover, investigating the relationship between key aspects of plant growth and reproduction and the conditions of the habitat they occupy, including the availability of all essential resources in the local environment, is an important aspect of research in biological invasions. To identify the characteristics of successful invaders, a comparison of closely related native and alien species, especially when they occur in similar habitats, is illuminating because such an approach helps to minimize bias related to phylogenetic distance and habitat affinities (Pyšek and Richardson 2007).

The genus *Impatiens* L., belonging to the family Balsaminaceae, comprises approximately 1000 species (Grey-Wilson 1980; Fischer 2004). Many of them are appreciated because of their exceptional ornamental qualities, and the cultivation of certain species has contributed to spectacular invasions worldwide, including in Europe (Adamowski 2008). Non-native *Impatiens* species in Europe differ in their origins, secondary range distributions, and levels of invasiveness. The most widely distributed non-native species in Europe is *Impatiens parviflora*, originating from the mountains of Central Asia, where it thrives along the banks of rivers and streams, on rocky mountain slopes, in damp shaded places, and in deciduous forests (Coombe 1956; Hejda 2012). The rate of *I. parviflora* spread is assessed to be moderate, likely associated with its low tolerance to severe frosts as well as moderate growth rate and seed production, and constraints on seed dispersal into suitable, shaded habitats (Perrins et al. 1993). *I. glandulifera* is another invasive species, originated from the Western Himalayas, where it is a component of high-altitude meadow and herbaceous plant communities at forest edges (Tanner et al. 2014). It spreads very rapidly (Perrins et al. 1993) and is considered particularly harmful to native ecosystems in Europe (EU 2017), hence it is the subject of numerous research projects, including those related to control measures (Hulme and Bremner 2006; Rusterholz et al. 2017; Kiełtyk and Delimat 2019; Najberek et al. 2020, 2022). The North American *I. capensis* occurs within its native range in the undergrowth of riparian forests, in wooded margins of marshes and peat bogs, as well as along roadside ditches and forest paths. It has established itself in several European countries as a naturalized or invasive species (Rewicz et al. 2022). The only native *Impatiens* species in Europe is *I. noli-tangere*, predominantly inhabiting damp woods as well as the edges of rivers, streams, and lakes (Hatcher 2003). In recent years, there has been a decrease in the abundance and population sizes of this species, along with a loss of its habitats, resulting in instances of large-scale extinctions (Tichý 1997; Preston et al. 2002). Furthermore, plants of the native species seldom re-emerged at locations from which they had disappeared (Hatcher 2003).

To date, research on interspecific coexistence in natural populations of the *Impatiens* genus in Europe has focused on *I. noli-tangere* and *I. parviflora*, as well as on *I. noli-tangere*, *I. parviflora*, and *I. glandulifera*. Studies comparing the first pair of species did not provide clear conclusions, as they revealed extensive habitat overlap between the native and non-native *Impatiens* species, with most environmental factors exhibiting greater variation in plots invaded by *I. parviflora* compared to those with *I. noli-tangere* (Vervoort and Jacquemart 2012). Conversely,

studies also demonstrated significant differences in the environmental preferences of both species (Godefroid and Koedam 2010). Research on the co-occurrence of three *Impatiens* species revealed a rather limited potential for coexistence under shared conditions (Čuda et al. 2014). Instead of forming mixed assemblages, the *Impatiens* species tend to coexist at separate microsites on a local scale. While the presence of *I. parviflora* does not negatively impact the native *I. noli-tangere*, the simultaneous occurrence of all three congeners may favour the spread of *I. glandulifera*, given its adverse effects on the population dynamics of both *I. noli-tangere* and *I. parviflora*. Studies comparing the native *I. noli-tangere* with the alien *I. capensis* in its secondary range have not been conducted thus far, particularly in the context of traits revealed by both species and natural environmental conditions under which their populations occur. To date, there have been no reports of co-occurrence of both *Impatiens* species in Europe. However, experimental studies suggest that these species share similar ecological requirements (Skálová et al. 2012). This overlap in ecological niches should be confirmed through field studies, assessing the environmental conditions of each species' habitat. Suitable sites for such comprehensive investigations can be found in Poland, where *I. capensis* is at the edge of its European range and is recognized as an invasive species posing a threat to native biodiversity (Tokarska-Guzik et al. 2012; Adamowski et al. 2018). Simultaneously, as demonstrated by Rewicz et al. (2022), its Polish range is outside the climate niche for the species, indicating its high adaptability to new habitat conditions.

In contrast to long-established alien species in Poland, such as *I. parviflora* and *I. glandulifera*, *I. capensis* represents a relatively recent threat, with its invasion still in the early stages, currently limited to the northwestern edge of the country. The species was first recorded in 1987 (Pawlaczyk and Adamowski 1991), and since then, its continuous spread has been observed (Popiela et al. 2015; Adamowski et al. 2018). Within its secondary range, *I. capensis* has been recorded primarily in herbaceous communities along water bodies and watercourses, with less frequent occurrences in moist forests and shrublands. It also thrives in damp ruderal areas like roadsides (Pawlaczyk and Adamowski 1991; Matthews et al. 2015; Adamowski et al. 2018). Experimental studies on the environmental responses of *I. capensis* and *I. noli-tangere* (Skálová et al. 2012) have confirmed that these species are capable of coexisting, with *I. noli-tangere* acting as the weaker competitor. Furthermore, the close phylogenetic relationship between the two species (Yu et al. 2016) poses an additional threat, as it may lead to the possibility of hybridization when they co-occur (Tabak and von Wettberg 2008). In the context of the foregoing considerations, the question of whether it is possible for *I. capensis* to potentially encroach into the habitats of *I. noli-tangere*, which could accelerate the retreat of the native species from specific locations, is decidedly relevant. Here, not only the similarity of ecological niches of the two species will be important, but also potential differences in how various environmental factors affect their performance, particularly traits related to growth and reproduction, as these play a crucial role in shaping the coexistence patterns of native and invasive *Impatiens* species (MacDougall et al. 2009; Čuda et al. 2014).

The primary aim of the study was to examine the growth and reproduction of individuals of the native species *I. noli-tangere* and the alien species *I. capensis*, occurring in diverse natural environmental conditions, and to investigate whether specific environmental factors influence each species similarly, either positively or negatively. Moreover, we wanted to elucidate the determinants of potential habitat segregation between the two *Impatiens* species in their natural environment, as well

as to identify the key factors contributing to variations in growth and reproductive success among individuals within natural populations of each species. The research conducted addressed the following specific questions: (1) Do the environmental conditions under which *I. noli-tangere* occurs differ from those influencing *I. capensis*, or is the intraspecific variability of habitat conditions more significant? (2) What is the extent of variability in environmental factors within individual sites (microspatial habitat heterogeneity)? (3) Are there differences in the growth and reproductive traits of individuals of both species? (4) Which environmental factors are correlated with the traits of the individuals studied? Do the same factors influence vegetative and generative traits of the two *Impatiens* species?

Material and methods

Species studied

Impatiens noli-tangere L. (touch-me-not balsam) is an annual herb from 20 to 180 cm tall, featuring a simple or branched stem. Its leaves measure between 1.5 to 10 (12) cm in length and 1.5 to 4 cm in width, are typically ovate-elliptical to ovate-lanceolate or oblong in shape, with 7–16 (-20) teeth on each side, usually mucronate. The flowers are arranged in axillary racemes (Moore 1968; Pawlaczyk and Adamowski 1991; WFO 2024). The species can produce both cleistogamous and chasmogamous flowers. The former are small, 2–3 mm long, closed, obligatorily self-fertilized, the latter being larger of around (1.5-) 2.0–3.5 cm in size, protandrous, with three sepals and five petals, yellow with small brownish/red spots. Chasmogamous flowers continuously secrete nectar into a 6–12 mm long, curved spur, providing sustenance for small insects and larger ones with sufficiently long tongues (e.g., *Bombus hortorum*). Fruits develop within two weeks. The capsule is 5-chambered, linear, measuring 1.5 cm in length, and contains 1–9 seeds. *I. noli-tangere* is a circumboreal species; its native range spans temperate regions of Eurasia, extends from Alaska to Central Canada, and reaches into west-central California (POWO 2024). It occurs on damp to wet, nitrophilous soils, in fairly warm, and partially shaded situations. Phenotypic traits of the species can be affected by shading, moisture, and nutrient levels (Hatcher 2003). Germination occurs in central European woods from late February onwards, the lifecycle being typically completed by late November, with flowering occurring from early July to late August (Faliński 1986).

I. capensis Meerb. (orange balsam) is an annual plant, up to 20–150 (230) cm tall. It has a naked, translucent stem with swollen nodes, and is usually branching. The petiolate, spirally arranged leaves are ovate-elliptical, 3–10 cm long and up to 5 cm wide, with coarsely toothed margins, 5–12 (-14) teeth being located on each margin (Moore 1968; Pawlaczyk and Adamowski 1991; Tabak and von Wettberg 2008). The plant also produces two types of flowers: small, greenish closed cleistogamous flowers (self-crossing) and large, colourful chasmogamous flowers (outcrossing). The chasmogamous flowers, 20–35 mm long, protandrous, emerge singly or in clusters from the upper leaf axils. They possess a 5–9 mm long spur, bent at an angle of 180 degrees, and are predominantly orange with large reddish-brown spots (Schemske 1978; Matthews et al. 2015). The capsule is approximately 2 cm long with pale orange streaks. Mature seeds are dark brown, rough, ellipsoidal in shape, with a narrowed apex and base, and four strong, distinct ribs (Rewicz et al. 2020). *I. capensis* is native to North America. It occurs in nine European countries

(United Kingdom, France, Germany, Finland, Poland, Netherlands, Denmark, Belgium, and Switzerland) where its status ranges from accidentally introduced (casual) to naturalized to invasive or high-risk. Outside Europe, it is considered an alien species in the states of Washington and Oregon (USA), in British Columbia, Northern Mexico, and Japan (Perrins et al. 1993; Akiyama 2000; Zika 2006; Matthews et al. 2015; Rewicz et al. 2022). The species spreads spontaneously via autochory, ejecting seeds from capsules up to a distance of about 2 m (Hayashi et al. 2009). Over longer distances, dispersal occurs via river and stream water (hydrochory). *I. capensis* poses a threat to several natural habitats protected under the European Habitat Directive (Tokarska-Guzik et al. 2012; Rewicz et al. 2022). The species may effectively compete with native plants for pollinating insects, as studies have shown that its nectar contains more chemical compounds than that of *I. noli-tangere*, including geraniol and linalool, which attract bumblebees and honeybees. Simultaneously, field observations indicate that the two species share similar common pollinators (Jakubska-Busse et al. 2023; Rewicz et al. 2024) (Fig. 1).

Study sites

Fieldwork was conducted in August 2021 at four sites of *I. noli-tangere* and five sites of *I. capensis* in Poland. The selection of the study area was driven by the fact that *I. capensis* is found in Poland at the edge of its consolidated secondary range and is recognized as locally invasive. The species thrives in various habitat types and is noted for its rapid spread and high competitiveness against native species, including perennials (Tokarska-Guzik et al. 2012; Adamowski et al. 2018). The research sites selected varied in habitat conditions, particularly in terms of vegetation type and shading intensity, degree of anthropogenic pressure, and types of human interactions. The chosen sites encompass the observed habitat range for each of the species studied (Table 1).

Habitat conditions

The sites surveyed were characterized in terms of habitat conditions, taking into account the physicochemical properties of the soil, the degree of shading of the vegetation (assessed on a three-point scale, where 1 indicates no shading, 2 - light shading, 3 - heavy shading), the degree of anthropogenic pressure (assessed on a three-point scale, where 1 indicates minimal human impact on the habitat, 2 - moderate impact, 3 - strong impact), and the presence or absence of aphid feeding on the ten randomly selected *Impatiens* individuals, as well as damage caused by fungi (both binary variables).

In the vicinity of each individual plant selected for the study, three soil samples from the root zone (0–15 cm) were collected using Egner's soil sampler. The three samples were merged to form a combined sample intended for laboratory analyses. A total of 90 soil samples were collected to characterize habitat conditions, including 40 samples for *I. noli-tangere* and 50 for *I. capensis*. Soil moisture content was assessed manually *in situ*, employing a 4-point scale developed by the Soil Science Society of Poland (2017): (1) dry (the soil disintegrates into crumbles and dust, lacking coolness or moisture upon touch; visibly darkens upon wetting), (2) fresh (the soil feels cool, yet is devoid of moisture; darkens after wetting), (3) moist (the soil dampens fingers and tissue paper, yet does not release water upon compression; clayey, loamy, and some dusty soils exhibit plasticity; does not darken post-wetting), (4) wet (water seeps from the soil when squeezing aggregates, causing the soil to smear).

Figure 1. **A–D** *Impatiens noli-tangere* (**A, C**) and *I. capensis* (**B, D**) (photo **A–C** Myśliwy, **D** Rewicz).

In the laboratory, soil samples underwent natural drying at room temperature, followed by sieving to remove particles larger than 1 mm in diameter. The sieved material was used for assessing the organic matter content (%), measured as loss on ignition at 550 °C, and pH, determined potentiometrically in 1 M KCl solution. Total carbon (C) and total nitrogen (N) contents (%) were determined using the CHNS/O FlashSmart (Thermo Scientific) elemental analyser. In the statistical analyses, only the C:N ratio was used as a measure of habitat fertility (an inversely proportional relationship). Additionally, the sieved material was used for preparing a solution for extraction of other soil elements in their easily leachable ionic forms. For this purpose, 10 g of dry soil from each sample were weighed into a

Table 1. Basic characteristics of *Impatiens noli-tangere* and *I. capensis* sites studied.

Species	Site with coordinates	Code	Type of habitat	Degree of shading	Degree of soil moisture	Degree of anthropogenic pressure	Main anthropogenic impacts
Impatiens noli-tangere	Sieradz N51.41641 E18.773301	Int_S	Dense forest	3	4	1	Asphalt-covered road nearby
	Recz N53.216917 E15.469056	Int_R	Dense forest	3	2	2	Adjacent asphalt-covered road and arable field, scattered litter in the forest
	Koszewko N53.258333 E14.905667	Int_K	Loose forest with clearings	2	3	1	Arable field nearby
	Binowo N53.325722 E14.648056	Int_B	Loose forest with clearings	2	3	1	Asphalt-covered road nearby
Impatiens capensis	Załom N53.438667 E14.702333	Ic_Z	Tall herbs with shrubs	1–2	2	2	Mowing in adjacent flood embankments
	Trzebieradz N53.675417 E14.44125	Ic_T	Dense forest	3	3–4	1	No direct human impact
	Szczecin-Zdroje N53.382861 E14.614944	Ic_SZ	Tall herbs	1	3–4	2	Tourists walking and fishing
	Święta N53.559556 E14.638889	Ic_Sw	Tall herbs	1	3	1	Asphalt-covered road nearby
	Police N53.557889 E14.570611	Ic_P	Tall herbs	1	3	3	Storage of garbage and biomass from adjacent allotment gardens

Explanations: the degree of shading: 1, no shading; 2, light shading; 3, heavy shading; the degree of soil moisture: 1, dry; 2, fresh; 3, moist; 4, wet (Soil Science Society of Poland 2017); the degree of anthropogenic pressure: 1, minimal human impact; 2, moderate impact; 3, strong impact.

plastic bottle. Subsequently, hydrochloric acid (100 cm^3 of 0.5 mol/dm^3 solution) was added, and the mixture was stirred for 1 hour on a rotary mixer. The mixture was then filtered through a sturdy funnel into a tightly sealed plastic container. The initial cloudy droplets were discarded. Similarly, a blank sample was prepared without soil, following the same procedure.

All solutions derived from the soil samples were stored at -80 °C until analysed. Levels (mg/kg) of calcium (Ca), sodium (Na), potassium (K), phosphorus (P), magnesium (Mg), zinc (Zn), copper (Cu), iron (Fe), manganese (Mn), silicon (Si), chromium (Cr), lead (Pb), nickel (Ni), titanium (Ti), and strontium (Sr) were determined with inductively coupled plasma optical emission spectrometry (ICP-OES) on the ICAP 7400 Duo instrument (Thermo Scientific) featuring a concentric nebulizer and cyclonic spray chamber. The analyses were performed using both radial and axial modes. Each sample, weighing a minimum of 0.1 g, was placed in pristine polypropylene vials. Subsequently, 5 ml of 65% HNO_3 (Suprapur, Merck) was added to each vial, every sample was left under a clean hood for 30 minutes of the pre-reaction time. Then, 1 ml of non-stabilized 30% H_2O_2 solution (Suprapur, Merck) was added to each vial and the samples, enclosed in Teflon vessels, were heated in a microwave digestion system at 180 °C for 35 minutes (with a 15-minute ramp to 180 °C followed by 20 minutes at 180 °C). After digestion, the samples were removed from the microwave apparatus and allowed to cool to room temperature. Subsequently, they were transferred into acid-washed

15 ml polypropylene sample tubes under a clean hood and were diluted 100× to facilitate ICP-OES measurements, with 250 µl of each digest being extracted for the analysis. A spike of the internal standard was used to achieve the final concentration of 0.5 mg/l Ytrium in the samples, along with the addition of 1 ml of 1% Triton (Triton X-100, Sigma). Following that, each sample was diluted to 10 ml with 0.075% nitric acid (Suprapur, Merck). The samples were then stored in a temperature-controlled refrigerator at 4 °C, pending analysis. Blank samples were prepared by adding 200 µl of concentrated nitric acid to empty tubes, followed by dilution with the procedure identical to that described above. A blank sample was analysed after each 10 measurements. Multi-element calibration standards (ICP multi-element standard solution IV, Merck) for Ca, Na, K, P, Mg, Zn, Cu, Fe, Mn, Si, Cr, Pb, Ni, Ti, and Sr were determined by using different concentrations of inorganic elements, following the procedure identical to that used for blanks and actual samples. All solutions were prepared using deionized water (Direct Q UV, Millipore, approximately 18.0 MΩ). The wave lengths (nm) were: 315.887 for Ca, 589.592 for Na, 766.490 for K,178.284 for P, 280.270 for Mg, 206.200 for Zn, 224.700 for Cu, 238.204 for Fe, 257.610 for Mn, 251.611 for Si, 205.560 for Cr, 220.353 for Pb, 231.604 for Ni, 336.121 for Ti, and 421.552 for Sr.

Species growth and reproduction traits

Our study on *Impatiens* involved traits associated with plant growth, reproduction, and overall functioning in response to environmental conditions, which collectively contribute to what is commonly referred to as 'performance.' At each site, 10 individuals of the *Impatiens* species were randomly selected for examination, resulting in a total of 40 specimens of *I. noli-tangere* and 50 specimens of *I. capensis*. For each individual, the following measurements were taken: 1) height of the main stem (cm), 2) number of nodes, 3) number of lateral branches of the main stem, 4) length of each of the three lower internodes (the designation "internode number one" refers to the internode closest to the ground, the subsequent internodes above it being labelled "internode number two" and "internode number three"), 5) number of flowers, including flower buds, 6) number of fruits (mature and immature combined), and 7) length and width of three leaves from standardized locations within each plant (leaf number one is the uppermost fully developed leaf on the main stem; leaf number two is the leaf emerging from the main stem node where the highest lateral branch originates; leaf number three is the longest leaf from the longest lateral branch). The leaf numbering adopted was consistently applied, since it is crucial in leaf comparisons to specify which leaves are being compared, as demonstrated by Whitfield and Toczydlowski (2020).

Data analysis

Normality of variable distributions was assessed using the Shapiro-Wilk test. The null hypothesis of the underlying normal distribution was rejected (data not presented). Correlation analyses involved the non-parametric Spearman's rank test. Following Meissner (2010), the following ranges of the correlation coefficients were used to assess the strength of correlation: 0.20 and lower – a very poor correlation; 0.21–0.39 – a weak correlation; 0.40–0.69 – a moderate correlation; 0.70–0.89 – a strong correlation; 0.90 and higher – a very strong correlation.

The Kruskal-Wallis test and median test, with post hoc comparisons of the mean ranks of all pairs of groups, were used to test for differences between the study sites, while the *Impatiens* species studied were compared using the Mann-Whitney U test with correction for continuity. All the analyses mentioned were performed using Statistica v. 13.1 for Windows (StatSoft Inc. 2013).

The impact of environmental factors on *Impatiens* traits was evaluated using the software CANOCO v. 4.5 (ter Braak and Šmilauer 2002). Patterns of species traits combination in relation to environmental factors were explored through multivariate redundancy analysis (RDA), following the detection of a linear structure in the dependent data by detrended correspondence analysis (DCA). The significance and importance of environmental factors were determined using the Monte Carlo permutation test and the stepwise forward selection of explanatory variables, both available in CANOCO. Collinearity (redundancy) among independent variables was examined using the variance inflation factor analysis (VIF analysis provided in CANOCO). A substantial redundancy is considered to occur when VIF > 20. The high autocorrelation among these variables rendered the canonical coefficients unstable, thus precluding meaningful interpretation. Variables exhibiting high VIF values should be excluded from subsequent analyses (ter Braak 1986). Additionally, the agglomerative hierarchical cluster analysis (UPGMA with Euclidean distance) was applied to the matrix of mean trait values of individual locations, using the software MVSP 3.2 (Kovach 2010).

Results

Combined habitat conditions of the two *Impatiens* species

The *I. noli-tangere* stations were located in forest communities, at sites that were strongly (Sieradz, Recz) or slightly (Koszewko, Binowo) shaded, characterized by a low and moderate human pressure. *I. capensis* was more frequent in open, unshaded habitats, subjected to a low (Święta) and moderate (Załom, Szczecin-Zdroje) or even strong (Police) human pressure. One site with alien species (Trzebieradz) was located in a relatively dense forest, characterized by strong shading and a low human influence (Table 1).

The habitats of both *Impatiens* species featured moist to wet soils; however in Recz and Załom (the respective sites for *I. noli-tangere* and *I. capensis*), the habitat was noticeably dried out. The physicochemical properties of soil at all the examined *Impatiens* sites showed a large range of values (Figs 2, 3, Suppl. material 1: table S1) and many significant between-site differences (Suppl. material 1: table S2). The soil pH at five sites was acidic, with mean pH values ranging from 3.9 (very acidic) to 5.6 (slightly acidic). At four sites, the soil pH was neutral, with mean values ranging from 6.7 to 7.2, the highest average being at the Koszewko site (Fig. 2A). The largest significant differences in the soil pH were found between the Binowo and Koszewko sites (Z-value = 6.5). Five sites featured organic soils (the mean soil organic matter content ranged from 29.1% to 69.2%); the remaining sites showed mineral or mineral-organic soils containing, on average, 5.6–6.5% and 11.1–11.4% organic matter, respectively (Fig. 2B), the largest significant differences being revealed between the Załom and Święta sites (Z-value = 6.3). The soil fertility, expressed as the inverse of the total carbon to nitrogen content ratio (C:N), encompassed a wide range. The mean C:N values ranged from 10.7 (the most fertile soils at Koszewko) to 23.3 (the poorest soils at Trzebieradz) (Z-value = 6.7) (Fig. 2C).

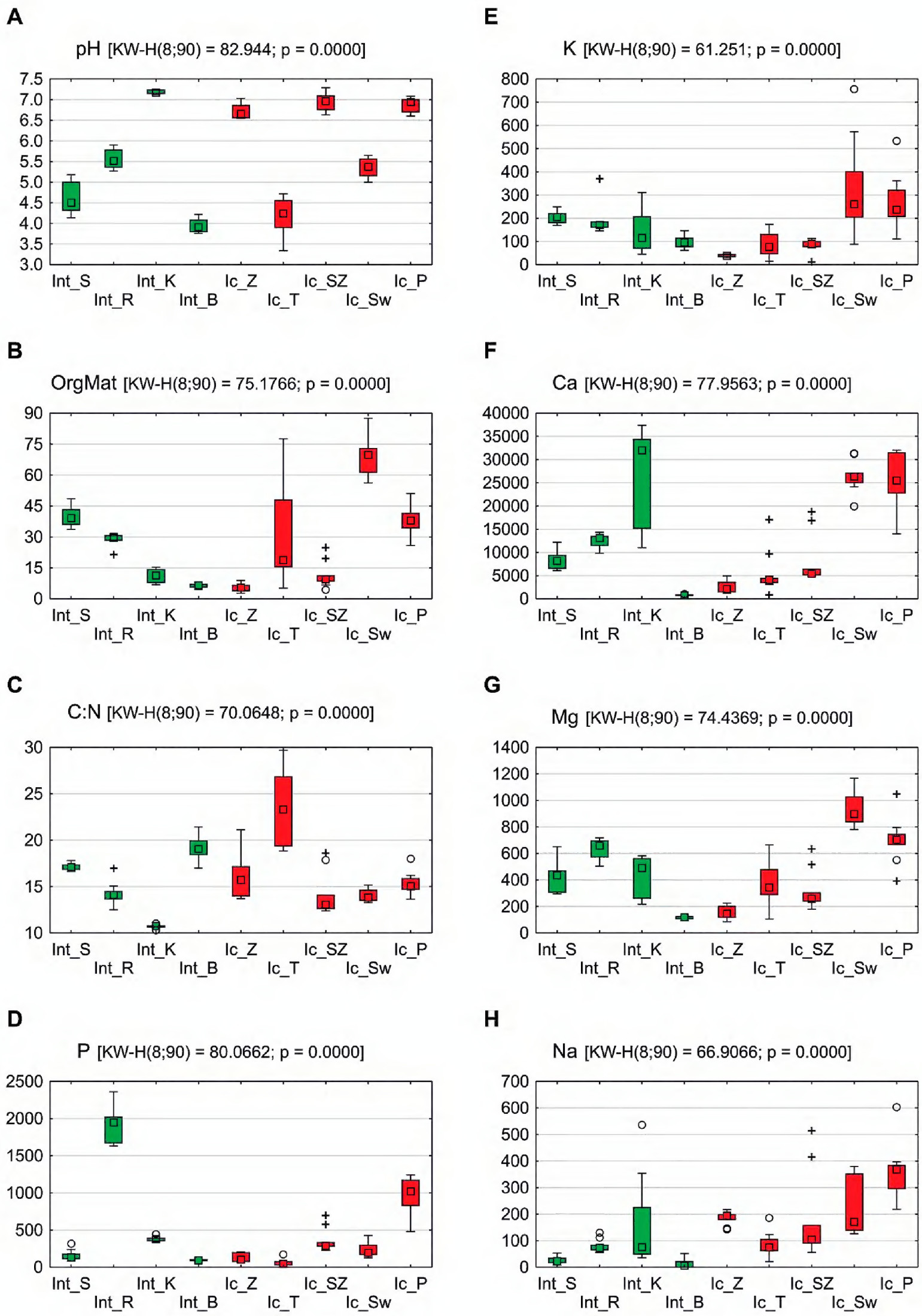

Figure 2. A–H Box and whiskers plots depicting selected soil parameters at the *Impatiens noli-tangere* (Int, green) and *I. capensis* (Ic, red) sites studied. Results of Kruskal-Wallis tests are given as H and p values. The box length represents the interquartile range, with the median indicated by small squares. Outlier values are represented by circles, crosses denoting extreme values. OrgMat, soil organic matter content. Complete names of sites are given in Table 1.

The widest ranges of soil contents were found in: calcium (mean values ranging from 772.6 mg/kg at Binowo to 26,605.1 mg/kg at Koszewko [Fig. 2F], Z-value = 5.9), iron (mean values ranging from 552.1 mg/kg at Załom to 10,014.1 mg/kg at Recz [Fig. 3A], Z-value = 6.1), phosphorus (mean values ranging from 56.5 mg/kg at

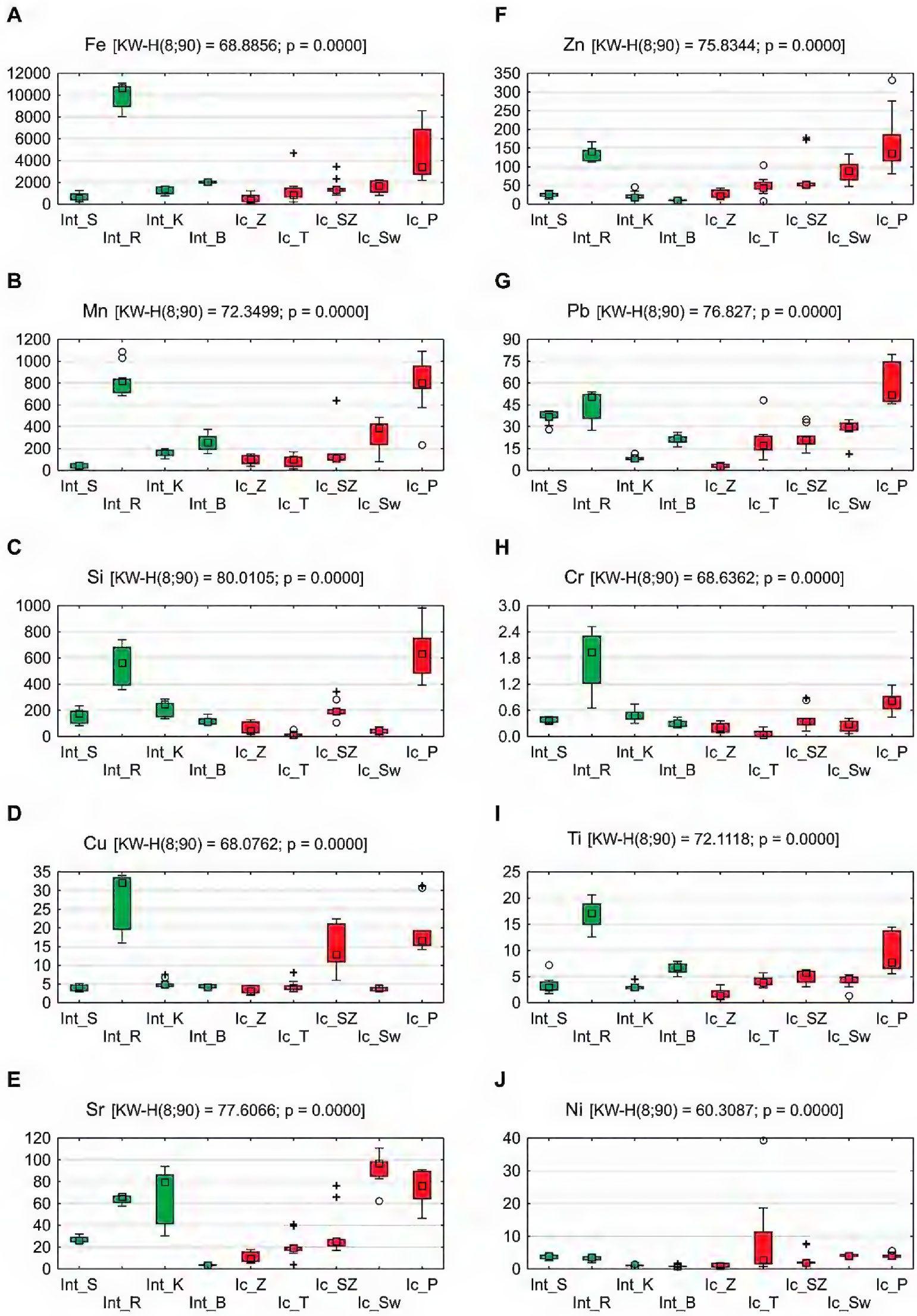

Figure 3. A–J Box and whiskers plots depicting soil contents of selected microelements at sites supporting *Impatiens noli-tangere* (Int, green) and *I. capensis* (Ic, red). Results of Kruskal-Wallis tests are given as H and p values. The box length represents the interquartile range, with the median indicated by small squares. Outlier values are represented by circles, crosses denoting extreme values. Complete names of sites are given in Table 1.

Trzebieradz to 1,937.1 mg/kg at Recz [Fig. 2D], Z-value = 6.6), magnesium (mean values ranging from 116.9 mg/kg at Binowo to 933.7 mg/kg at Święta [Fig. 2G], Z-value = 6.4), manganese (mean values ranging from 43.9 mg/kg at Sieradz to 829.2 mg/kg at Recz [Fig. 3B], Z-value 6.1), and silicon (mean values ranging from

15.8 mg/kg at Trzebieradz to 653.5 mg/kg at Police [Fig. 3C], Z-value = 6.4). The mean soil potassium content ranged from 38.8 mg/kg at Załom site to 329.7 mg/kg at Święta (Z-value = 5.5) (Fig. 2E). The highest relative coefficients of variation were found in the soil sodium content (Suppl. material 1: table S1). The lowest mean sodium concentration was recorded at Binowo (12.6 mg/kg), the highest mean concentration being found at Police (356.3 mg/kg; Z-value = 6.2) (Fig. 2H). Among the soil trace elements studied, the highest significant differences between the sites were observed in copper, strontium, and nickel (Suppl. material 1: table S2). The mean soil copper content ranged from 3.4 mg/kg at Załom to 27.3 mg/kg at Recz (Z-value = 5.5) (Fig. 3D). The mean soil strontium content ranged from 3.6 mg/kg at Binowo to 93.1 mg/kg at Święta (Z-value = 6.5) (Fig. 3E). The mean soil nickel content ranged from 1.0 mg/kg at Binowo to 9.2 mg/kg at Trzebieradz (Z-value = 3.5) (Fig. 3J). The highest mean soil zinc and lead contents were found at Police (163.6 mg/kg and 58.9 mg/kg, respectively), the lowest contents of the elements being recorded at Binowo (10.1 mg/kg; Z-value = 6.1) and Załom (3.1 mg/kg; Z-value = 6.6), respectively (Fig. 3F, G). The mean soil chromium content ranged from 0.1 mg/kg at Trzebieradz to 1.7 mg/kg at Recz (Z-value = 6.5) (Fig. 3H). The mean soil titanium content ranged from 1.7 mg/kg at Załom to 16.9 mg/kg at Recz (Z-value = 6.4) (Fig. 3I).

Comparison of *Impatiens noli-tangere* and *I. capensis* habitat conditions

Comparison of respective habitats supporting the two *Impatiens* species did not reveal significant differences in most parameters (Table 2, Suppl. material 1: table S3). Significant differences were observed only in the anthropogenic pressure and degree of shading as well as in the soil contents of a few elements: sodium (Na), silicon (Si), zinc (Zn), chromium (Cr), and nickel (Ni). The *I. noli-tangere* sites experienced a lower anthropogenic pressure, compared to the *I. capensis* sites (Z-value = -3.6). Shading at sites supporting *I. noli-tangere* was higher than that of *I. capensis* sites (Z-value = 5.7). The mean soil Na content at the *I. noli-tangere* sites was lower than that at the *I. capensis* ones (Z-value = -6.1); a similar pattern was revealed in the mean Zn content (Z-value = -3.7) and mean Ni content (Z-value = -2.3). In contrast, higher mean contents at the *I. noli-tangere* sites, compared to those supporting *I. capensis* were found in Si (Z-value = 3.2) and Cr (Z-value = 3.8). In addition, *I. noli-tangere* was more frequently infested by aphids than *I. capensis*, the difference being significant (Z-value = 5.2) (Suppl. material 1: table S3).

Species growth and reproduction traits

Due to the lack of sites where both studied *Impatiens* species coexist under identical habitat conditions, direct comparisons between the species were not made; instead, comparisons were conducted between populations of each species individually. The variability in species traits was notably greater for *I. noli-tangere* than for *I. capensis* (Table 3, Suppl. material 1: table S4). Among *I. noli-tangere* populations, significant differences were observed in plant height, number of nodes and lateral branches, length of the second and third internodes, as well as in the number of flowers and fruits, and in the length and width of individual leaves (Suppl. material 1: table S5). For *I. capensis*, statistically significant differences were found only in leaf size traits (Suppl. material 1: table S6).

Table 2. Basic statistical characteristics of soil parameters at the *Impatiens* species sites surveyed. CV, coefficient of variation.

Parameter	*Impatiens noli-tangere*				*Impatiens capensis*			
	mean	median	Range	CV (%)	mean	median	range	CV (%)
pH	5.3	5.2	3.8–7.2	23.4	6.0	6.6	3.3–7.3	18.6
Organic matter content (%)	21.8	18.4	4.5–48.6	65.3	30.7	22.6	2.8–87.6	83.0
C:N	15.3	16.7	10.3–21.4	21.6	16.5	14.9	12.4–29.7	25.3
P (mg/kg)	642.5	331.3	79.1–2359.0	120.7	348.4	204.3	7.3–1244.1	102.3
K (mg/kg)	162.6	167.0	45.2–370.5	47.0	160.5	102.7	12.2–755.7	97.2
Ca (mg/kg)	12035.0	10421.1	575.7–37403.5	89.1	13687.9	6241.5	792.1–32015.9	82.1
Mg (mg/kg)	400.6	451.2	94.3–717.3	52.2	496.5	406.5	85.5–1166.2	63.0
Na (mg/kg)	69.0	49.9	0.0–536.0	144.4	206.4	177.1	21.4–603.3	64.0
Si (mg/kg)	260.3	188.4	83.8–740.2	71.9	196.8	67.3	0.0–982.5	130.9
Fe (mg/kg)	3504.4	1723.3	198.3–11096.3	110.7	1885.6	1290.2	150.2–8566.6	97.0
Mn (mg/kg)	323.0	185.8	16.6–1089.0	97.5	301.6	141.0	14.1–1091.0	99.3
Zn (mg/kg)	48.5	21.6	8.2–166.7	108.2	80.5	56.3	7.9–331.7	80.1
Cu (mg/kg)	10.3	4.8	2.9–34.0	103.9	9.1	4.6	2.0–31.3	84.0
Pb (mg/kg)	27.8	27.0	6.4–53.9	54.2	26.6	23.5	1.3–79.7	76.6
Sr (mg/kg)	40.7	31.3	2.7–94.1	72.2	46.6	26.7	3.8–110.9	75.0
Cr (mg/kg)	0.7	0.5	0.2–2.5	93.5	0.4	0.3	0.0–1.2	87.4
Ni (mg/kg)	2.3	1.8	0.7–4.5	59.8	4.3	3.2	0.4–39.4	139.3
Ti (mg/kg)	7.5	5.4	1.7–20.6	78.9	4.9	4.6	0.6–14.5	61.5

Table 3. Basic statistical characteristics of growth and reproduction traits of native *Impatiens noli-tangere* and alien *I. capensis* in Poland. Full names of species traits: Height, height of the main stem (cm); NodNo., number of nodes; BraNo., number of lateral branches of the main stem; Int1L, length of first internode (closest to the surface of the ground); Int2L, length of second internode; Int3L, length of third internode; FloNo., sum of flowers and flower buds; FruNo., number of fruits (mature and immature combined); L1L, length of leaf number one; L1W, width of leaf number one; L2L, length of leaf number two; L2W, width of leaf number two; L3L, length of leaf number three; L3W, width of leaf number three (three leaves from standardized locations within each plant).

Trait	*Impatiens noli-tangere*				*Impatiens capensis*			
	mean	median	range	CV (%)	mean	median	range	CV (%)
Height	80.30	65.00	38.00–169.00	48.22	133.24	139.00	68.00–195.00	22.92
NodNo.	10.50	10.00	4–18	31.84	13.84	14.00	10–19	16.86
BraNo.	5.65	4.00	2–15	62.68	11.04	11.00	8–18	20.37
Int1L	5.46	5.00	1.00–15.00	50.71	10.02	10.00	3.50–19.00	38.37
Int2L	8.30	7.00	2.00–19.00	58.15	13.58	14.00	6.00–21.00	23.55
Int3L	8.60	7.00	2.00–28.00	63.46	14.35	14.00	6.00–24.00	26.02
FloNo.	53.15	27.00	0–217	120.05	95.32	83.50	10–263	57.12
FruNo.	14.05	6.00	0–62	126.73	22.64	20.50	5–65	57.37
L1L	3.23	2.90	2.10–6.85	30.96	3.90	3.80	2.40–6.20	25.33
L1W	1.85	1.80	1.00–3.50	28.38	2.02	2.03	1.15–3.05	25.43
L2L	5.28	3.20	1.50–14.60	65.26	5.95	6.00	2.80–8.50	23.01
L2W	2.60	2.20	1.10–6.60	51.68	2.81	2.80	1.50–4.25	20.53
L3L	5.11	4.55	2.10–11.50	48.60	5.55	5.58	2.40–8.10	24.72
L3W	2.52	2.25	1.20–5.60	40.91	2.73	2.83	1.20–4.10	25.42

Among the populations of *I. noli-tangere* studied, individuals from Koszewko stand out by showing significantly higher values for many of the traits determined; compared to the overall species mean, the Koszewko individuals were on average taller (138.4 cm and 80.3 cm, respectively), featured higher mean numbers of nodes (14.5 and 10.5, respectively), lateral branches (10.0 and 5.7, respectively), flowers (146.6 and 53.2, respectively), and fruits (41.8 and 14.1 respectively); their

leaves No. 2 were longer (10.0 cm and 5.3 cm, respectively) and wider (3.8 cm and 2.6 cm, respectively); similarly, leaves No. 3 were longer (8.5 cm and 5.1 cm, respectively) and wider (3.9 cm and 2.5 cm, respectively). On the other hand, the *I. capensis* population from Trzebieradz stands out as showing lower values of the traits than those found in the remaining populations. The Trzebieradz means compared to the overall species means show them to be shorter (89.5 cm and 133.2 cm, respectively), to produce fewer flowers and buds (50.2 and 95.3, respectively), but to have longer leaves; for example, the mean length of leaf No. 1 at Trzebieradz was 5.1 cm, compared to the species average of 3.9 cm (Table 3, Suppl. material 1: table S4). These differences are further highlighted by the cluster analysis dendrogram for sites, based on the traits of individual growth and reproduction: the division into two clusters corresponding to the two *Impatiens* species was disrupted at Koszewko and Trzebieradz. Individuals of *I. noli-tangere* from Koszewko were found to be most similar in terms of the traits determined to individuals of *I. capensis* from the Szczecin-Zdroje, while individuals of *I. capensis* from Trzebieradz were most similar in their traits to individuals of *I. noli-tangere* from Binowo (Fig. 4).

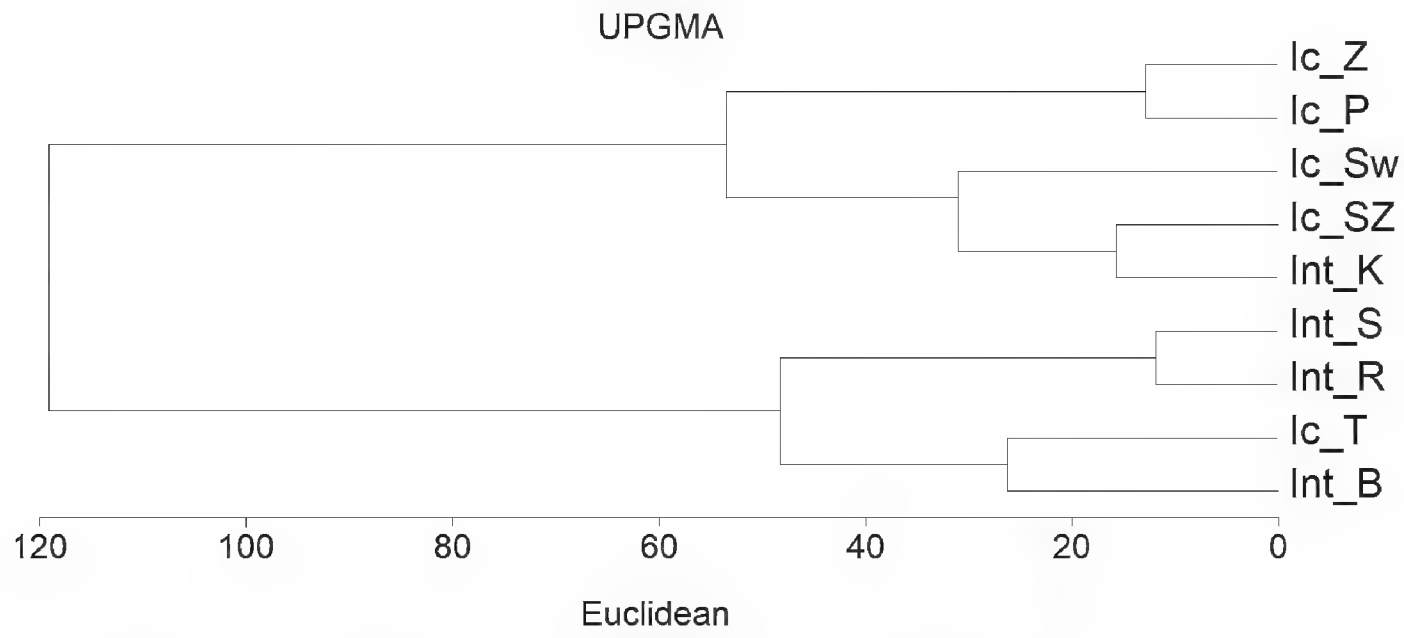

Figure 4. Results of Euclidean distance-based cluster analysis (UPGMA) for *Impatiens noli-tangere* (Int) and *I. capensis* (Ic) populations studied. Full site names are given in Table 1.

Patterns of specimen and trait distribution in relation to environmental factors

The multivariate redundancy analysis included initially all the 23 environmental factors. However, upon assessing the co-linearity among the explanatory variables, it became necessary to exclude four of them (strontium, magnesium, iron, and titanium) from further analyses, as their variance inflation factors exceeded acceptable thresholds (VIF > 20). After the reduction, the RDA results showed the remaining 19 environmental variables to account for 73.7% of the total variation in the dataset of *Impatiens* traits (Suppl. material 1: table S7). Results of the stepwise forward selection revealed only six variables to be statistically significant: the level of shading (Shading), the degree of anthropogenic pressure (Anthrop), the soil pH, the aphid infestation (Aphids), the degree of soil moisture (Moisture), and the soil calcium content (Ca). Together, they accounted for 68% of the total variance, with the level of shading making the highest contribution (43%) (Table 4).

Each solid arrow on the resultant RDA diagram indicates the direction of increasing values of each environmental variable. Samples (*Impatiens* specimens)

Table 4. Forward selection of explanatory variables with the significance test of habitat parameters explaining variance in *Impatiens* specimens' data; results highlighted in bold are statistically significant at $p \leq 0.05$.

No.	Variable /Code	Lambda A	Explained data variance [%]	*p*-value
1.	**Vegetation shading /Shading**	**0.43**	**43**	**0.002**
2.	**Anthropogenic pressure /Anthrop**	**0.08**	**8**	**0.002**
3.	**Soil pH /pH**	**0.07**	**7**	**0.004**
4.	**Presence of aphid feeding /Aphids**	**0.04**	**4**	**0.002**
5.	**Soil moisture /Moisture**	**0.04**	**4**	**0.002**
6.	**Soil Ca content /Ca**	**0.02**	**2**	**0.016**
7.	Soil organic matter content /OrgMat	0.01	1	0.064
8.	Soil Ni content /Ni	0.01	1	0.108
9.	Soil Cr content /Cr	0.01	1	0.106
10.	Soil Mn content /Mn	0.01	1	0.124
11.	Soil Na content /Na	0.01	1	0.280
12.	Soil C:N ratio /C:N	0.01	1	0.650
13.	Soil Si content /Si	0.00	0	0.176
14.	Soil Cu content/ Cu	0.00	0	0.256
15.	Soil P content /P	0.00	0	0.372
16.	Soil K content/ K	0.00	0	0.608
17.	Presence of fungi damage /Fungi	0.00	0	0.654
18.	Soil Pb content /Pb	0.00	0	0.694
19.	Soil Zn content /Zn	0.00	0	0.924

positioned in the direction indicated by the arrowheads of individual environmental variables were linked with relatively high values of these environmental variables as opposed to the samples located in the opposite direction that were associated with relatively low values (Fig. 5).

The distance between sample points in the ordination space reflects the dissimilarity of the specimen's trait composition, measured by the Euclidean distance. Samples that are closer to each other are more similar than those that are more distant. The right-hand side of the ordination diagram groups mainly *I. noli-tangere* individuals. They were associated with a stronger shading (forest areas), a lower anthropogenic pressure, a lower soil pH, an increased soil moisture, and a relatively lower soil calcium concentration. These individuals were also more frequently affected by aphid attacks. The left-hand side of the diagram shows more scattered individuals of *I. capensis*; these were primarily associated with a weaker shading (open-terrain areas), a higher anthropogenic pressure, a relatively higher soil pH and calcium content, and a decreased soil moisture. The upper part of the left-hand side of the ordination space shows primarily a grouping of individuals from a single *I. noli-tangere* site (Koszewko). These individuals were associated with soils characterized by the highest pH and calcium content (Fig. 5) which were also an exceptionally fertile habitat (the lowest C:N ratio; Fig. 2C).

A comparison of the RDA results for individual *Impatiens* species separately revealed significant differences in the relationships between their growth and reproduction traits in relation to habitat factors. For the native *I. noli-tangere*, following removal of the environmental variables with variance inflation factors exceeding acceptable thresholds, the remaining 16 factors explained 86.4% of the variation in the traits of the individuals studied. Five factors proved statistically significant: the soil

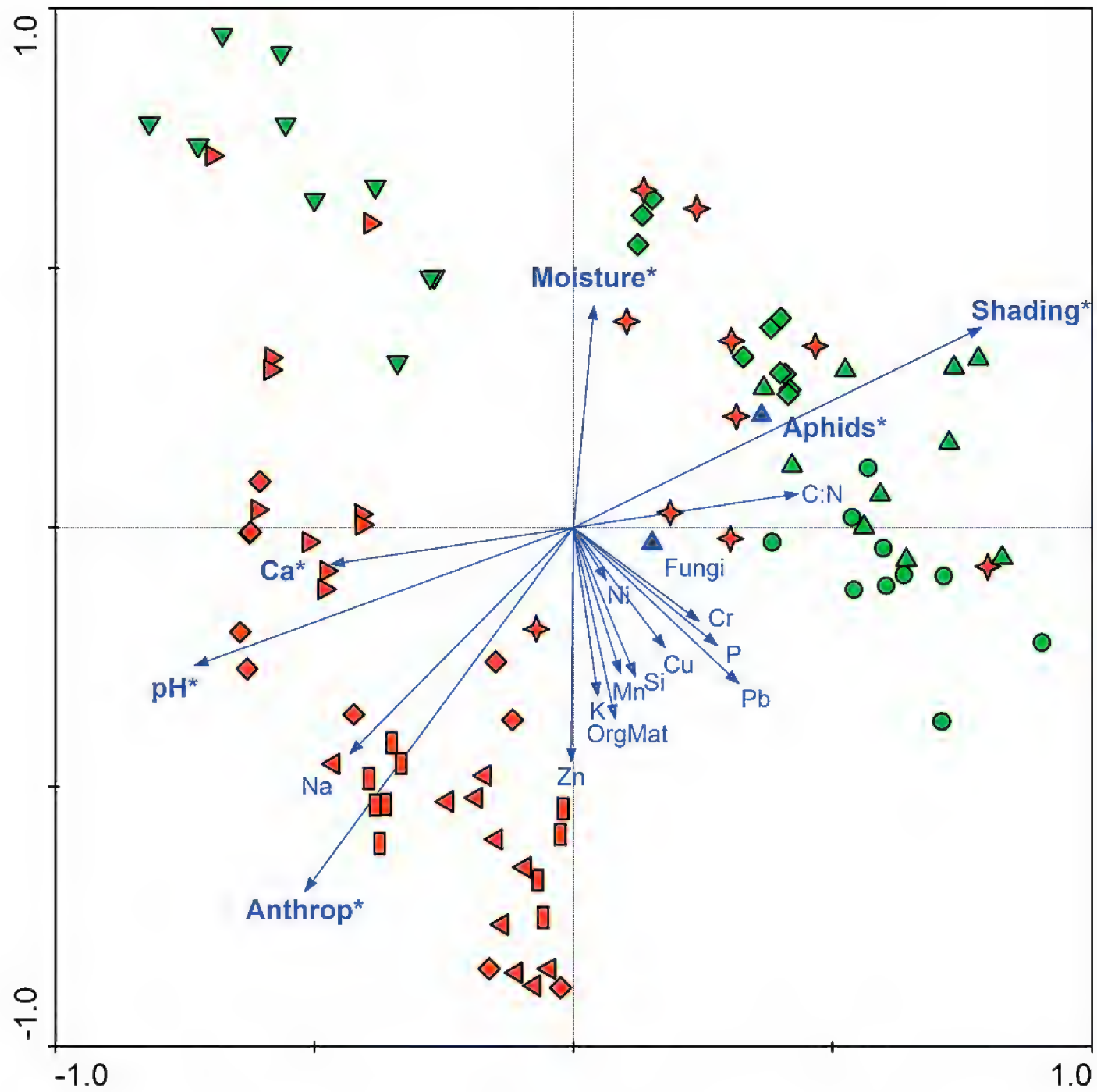

Figure 5. Ordination plot of *Impatiens* specimens (green and red symbols for *Impatiens noli-tangere* and *I. capensis*, respectively) and environmental variables (blue arrows for numerical and ordinal, blue triangles for nominal) along the first two RDA axes; significant variables are marked with asterix; various symbols are used to indicate individual sites: green circles for Recz, green up-triangles for Sieradz, green diamonds for Binowo, green down-triangles for Koszewko, red left-triangles for Police, red right-triangles for Szczecin-Zdroje, red diamonds for Święta, red boxes for Załom, and red stars for Trzebieradz. Full names of variables are given in Table 4.

Pb content, the habitat fertility expressed as the inverse of the carbon-to-nitrogen ratio, the degree of shading as well as the soil Ca content and pH. Taken together, these factors accounted for a substantial part (up to 84%) of the trait variation, Pb (56%) and habitat fertility (21%) being the most important (Table 5). The RDA results for the invasive *I. capensis* indicated that, after the necessary removal of two environmental variables due to their high variance inflation factors, the remaining 21 variables explained 70.7% of the variation in the growth and reproduction trait composition of the individuals. The statistically significant variables included the degree of shading, the anthropogenic pressure, the aphid infestation as well as the soil moisture content and pH. These significant variables collectively explained 57% of the variation, shading being the most important at 29% (Table 6).

Ordination plots of *I. noli-tangere* and *I. capensis* specimen traits and environmental variables (Figs 6, 7, respectively) illustrate how the combination of habitat factors influences trait patterns of both species. The vertical projections of the dashed arrows' tips (arrowheads representing individual features) onto the solid arrows indicate the optimized values of each environmental variable in relation to

Table 5. Forward selection of explanatory variables with the significance test of habitat parameters explaining variance in *Impatiens noli-tangere* specimens' data; results highlighted in bold are statistically significant at $p \leq 0.05$.

No.	Variable /Code	Lambda A	Explained data variance [%]	*p*-value
1.	**Soil Pb content /Pb**	**0.56**	**56**	**0.002**
2.	**Soil C:N ratio /C:N**	**0.21**	**21**	**0.002**
3.	**Vegetation shading /Shading**	**0.03**	**3**	**0.006**
4.	**Soil Ca content /Ca**	**0.02**	**2**	**0.042**
5.	**Soil pH /pH**	**0.02**	**2**	**0.034**
6.	Soil Cr content /Cr	0.01	1	0.110
7.	Soil Si content /Si	0	0	0.296
8.	Soil organic matter content /OrgMat	0.01	1	0.550
9.	Soil Mn content /Mn	0	0	0.462
10.	Soil K content /K	0	0	0.720
11.	Presence of aphid feeding /Aphids	0	0	0.786
12.	Presence of fungi damage /Fungi	0	0	0.862
13.	Soil Na content /Na	0	0	0.954
14.	Soil moisture /Moisture	0	0	0.926
15.	Soil Ni content /Ni	0	0	0.986
16.	Anthropogenic pressure /Anthrop	0	0	1.000

Table 6. Forward selection of explanatory variables with the significance test of habitat parameters explaining variance in *Impatiens capensis* specimens' data; results highlighted in red are statistically significant at $p \leq 0.05$.

No.	Variable /Code	Lambda A	Explained data variance [%]	*p*-value
1.	**Vegetation shading /Shading**	**0.29**	**29**	**0.002**
2.	**Anthropogenic pressure /Anthrop**	**0.07**	7	**0.020**
3.	**Presence of aphid feeding /Aphids**	**0.08**	**8**	**0.014**
4.	**Soil moisture /Moisture**	**0.06**	**6**	**0.030**
5.	**Soil pH /pH**	**0.07**	7	**0.010**
6.	Soil Ca content /Ca	0.02	2	1.630
7.	Soil P content /P	0.01	1	1.180
8.	Soil Mn content /Mn	0.01	1	1.610
9.	Soil Ni content /Ni	0.01	1	1.000
10.	Soil organic matter content /OrgMat	0.02	2	1.790
11.	Soil Si content /Si	0.01	1	0.920
12.	Soil Cu content /Cu	0.02	2	2.860
13.	Soil Na content /Na	0.01	1	0.660
14.	Soil C:N ratio /C:N	0.01	1	0.930
15.	Soil Zn content /Zn	0	0	0.640
16.	Soil Fe content /Fe	0.01	1	0.530
17.	Soil K content /K	0	0	0.30
18.	Presence of fungi damage /Fungi	0	0	0.210
19.	Soil Cr content /Cr	0	1	0.140
20.	Soil Ti content /Ti	0.01	1	0.140
21.	Soil Pb content /Pb	0	0	0.040

the optimized values of species traits. This does not merely reflect simple correlations (as shown in Suppl. material 1: tables S8, S9), but results from the interaction of all the explanatory variables together (conditional effect). Considering only the statistically significant environmental variables, all traits of *I. noli-tangere* were positively correlated with the soil pH, calcium content, and habitat fertility expressed as the inverse of the carbon-to-nitrogen ratio, while they were negatively correlated

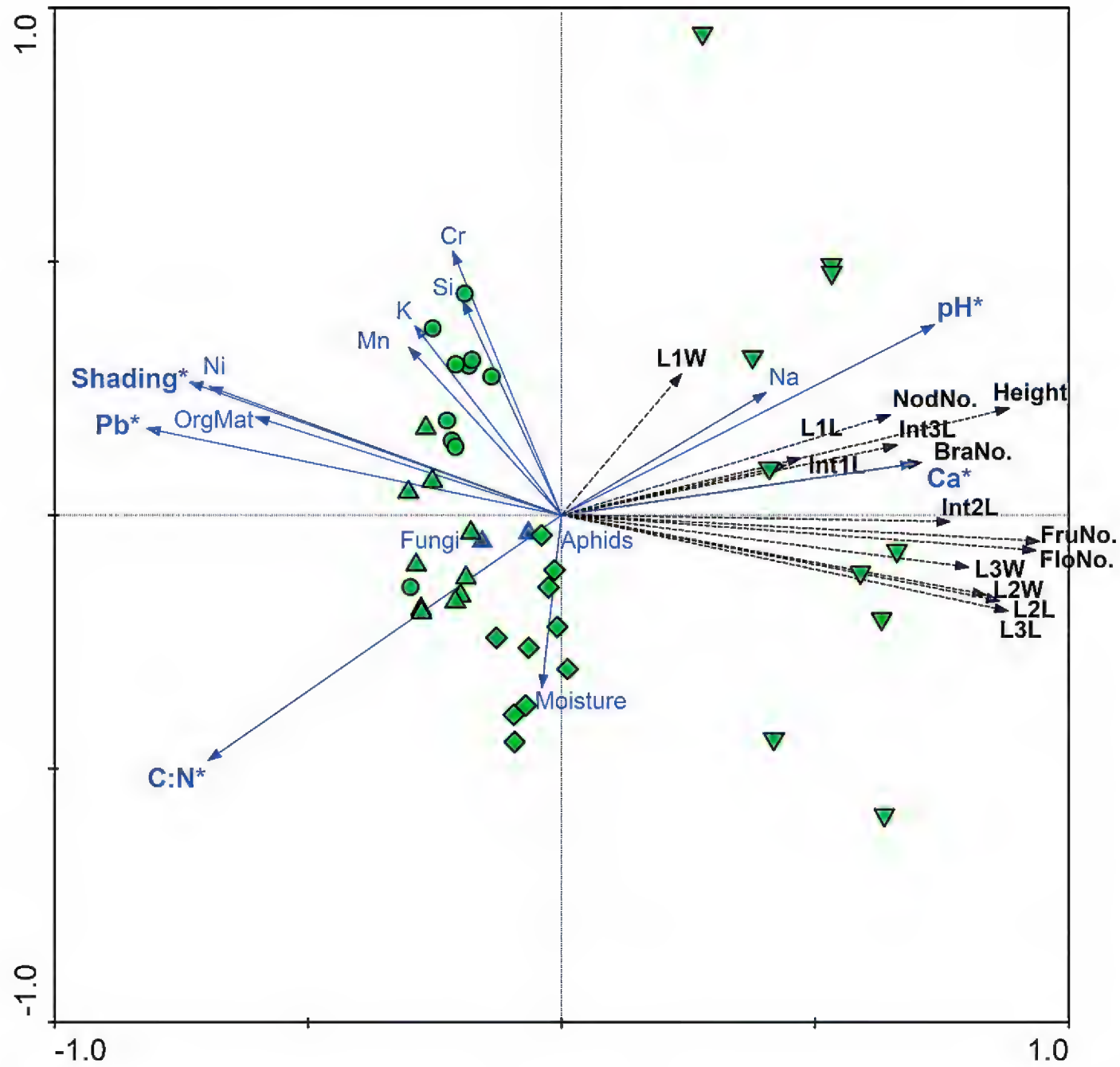

Figure 6. Ordination plot of *Impatiens noli-tangere* specimens (green symbols), species traits (black dashed arrows) and environmental variables (blue solid arrows for numerical and ordinal, blue triangles for nominal) along the first two RDA axes; significant variables are marked with asterisk; various symbols are used to indicate individual sites: circles for Recz, up-triangles for Sieradz, diamonds for Binowo, down-triangles for Koszewko. Full names of species traits: Height, height of the main stem (cm); NodNo., number of nodes; BraNo., number of lateral branches of the main stem; Int1L, length of first internode (closest to the ground); Int2L, length of second internode; Int3L, length of third internode; FloNo., number of flowers, including flower buds; FruNo., number of fruits; L1L, length of leaf number one; L1W, width of leaf number one; L2L, length of leaf number two; L2W, width of leaf number two; L3L, length of leaf number three; L3W, width of leaf number three (three leaves from standardized locations within each plant). Full names of variables are given in Table 5.

with the soil lead (Pb) content and the degree of shading (Fig. 6). For *I. capensis*, the direct relationships were obtained for the soil pH and degree of anthropogenic pressure with traits related to the individual size (stem height, number of nodes, internode length) as well as the number of flowers and fruits. Additionally, the soil moisture and the degree of shading were positively correlated with the leaf size (width and length of leaves No. 1–3). Inversely proportional relationships involved the impact of aphid infestation and the degree of shading on traits related to the plant size as well as the numbers of flowers and fruits (Fig. 7).

Differences in the impact of habitat conditions on the traits of the two *Impatiens* species were further confirmed by the direction of correlations shown by the linear Spearman rank correlation analysis (Suppl. material 1: tables S8, S9). The *I. noli-tangere* populations studied grew only in habitats experiencing low and moderate levels of human disturbance, and most of the traits examined for this species were

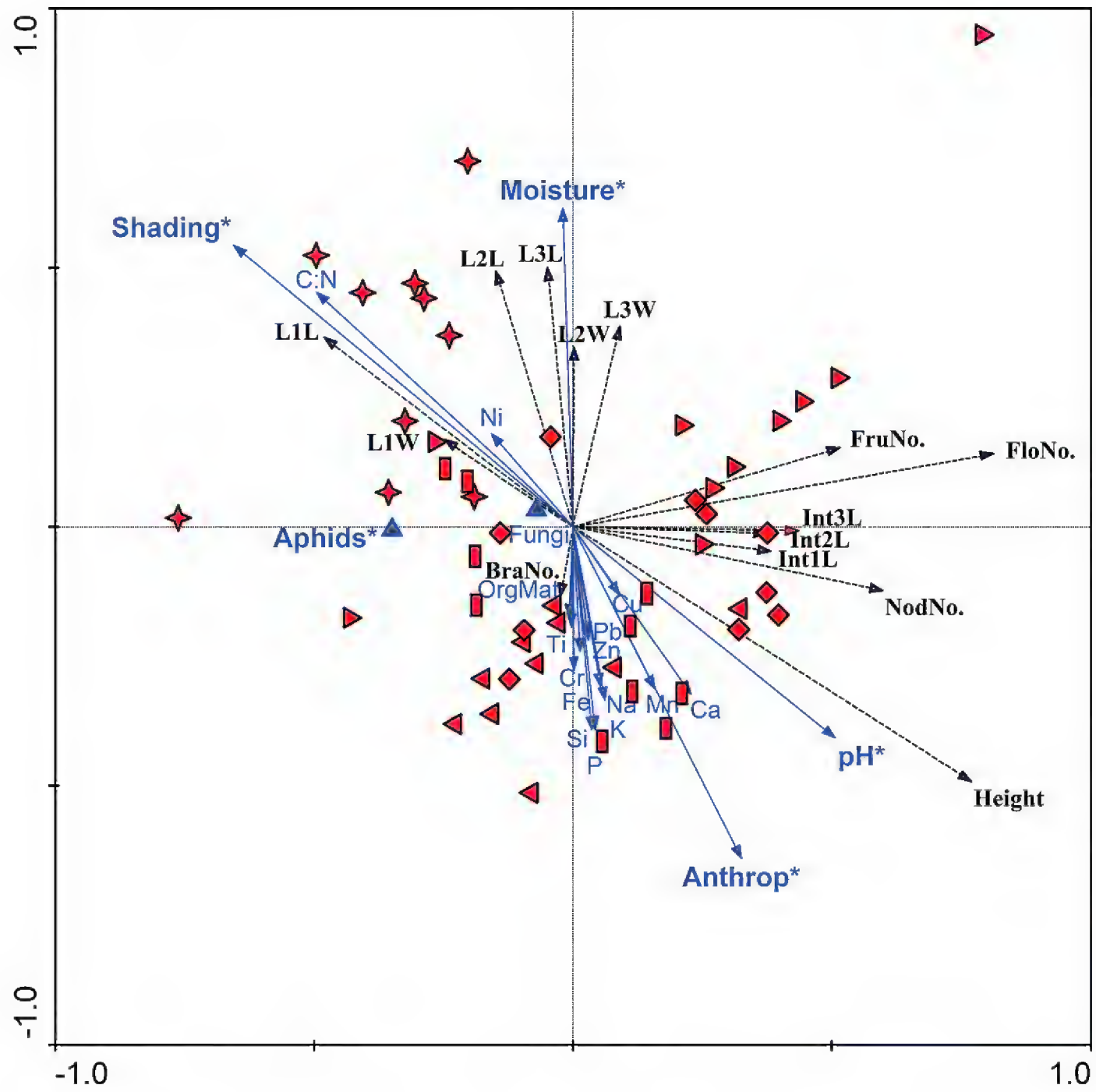

Figure 7. Ordination plot of *Impatiens capensis* specimens (red symbols), species traits (black dashed arrows) and environmental variables (blue solid arrows for numerical and ordinal, blue triangles for nominal) along the first two RDA axes; significant variables are marked with asterisk; various symbols are used to indicate individual sites: left-triangles for Police, right-triangles for Szczecin-Zdroje, diamonds for Święta, boxes for Załom, and stars for Trzebieradz. Full names of species traits are given in Fig. 6. Full names of variables are given in Table 6.

negatively correlated with anthropogenic pressure. Notably, there was a significant negative relationship with the number of flowers and fruits as well as with leaf size. In contrast, the degree of anthropogenic pressure was moderately positively correlated with the stem height of *I. capensis*, and correlated weakly positively with the first internode length. The width and length of leaves of *I. capensis*, however, were negatively correlated with the degree of anthropogenic pressure. Shading was inversely related to all the *I. noli-tangere* traits considered. Except for the influence of shading on the number of stem branches, the correlations were statistically significant and, in most cases, strong. The stem height of *I. capensis* was also strongly negatively correlated with shading. However, unlike the native species, the length and width of leaves were positively correlated with shading, the relationships being weaker but still significant. The soil pH was positively correlated with the stem height of both *Impatiens* species. The main differences lie in the number of branches and leaf sizes: for *I. noli-tangere*, the soil pH moderately positively affected these traits, the correlation being negative in *I. capensis*. Habitat fertility expressed as the inverse of the carbon-to-nitrogen ratio was positively correlated with the height, number of nodes, and number of flowers of both species. However, differences mainly concerned the

leaf size: for *I. noli-tangere*, the relationships were also positive but mostly not significant, whereas for *I. capensis*, the habitat fertility was negatively correlated with the leaf width and length, the correlations being mostly moderate. The main differences in correlations between the soil element contents and the traits of the two *Impatiens* species concerned several elements. Lead correlated significantly negatively with almost all traits of the native *Impatiens*, and many of these correlations were strong. For *I. capensis*, significant negative correlations were only weak to moderate, and were limited to the leaf size. Additionally, the relationship between the soil Pb content and the number of branches on the main stem differed between the species: the correlation was moderate and inverse in *I. noli-tangere*, while it was moderate and direct in *I. capensis*. The soil Ca content correlated positively with almost all traits of *I. noli-tangere*, but significant moderately strong correlations were observed only for the stem height, number of nodes and branches, and the size of leaf No. 1. The stem size of *I. capensis* was also positively, albeit weakly to moderately, correlated with the soil Ca content; however, a negative relationship was observed with the leaf length. Other elements were not significant in multivariate analyses, but linear correlations revealed differences in the influence of the soil phosphorus, silicon, iron, manganese, copper, chromium, and titanium contents. The elements listed were generally more strongly negatively correlated with the leaf size in *I. capensis* than in the native species. Zinc was moderately negatively correlated with the internode length and the numbers of flowers and fruits in *I. noli-tangere*, while in *I. capensis*, these relationships were positive but mostly not significant. Nickel was negatively correlated with all traits of *I. noli-tangere*, most correlations being moderate, whereas in *I. capensis*, these were mainly not statistically significant, except for a moderate positive correlation with the number of branches and a weak positive correlation with the size of leaf No. 1 (Suppl. material 1: tables S8, S9).

Discussion

Native species are constantly confronted with new ecological challenges many of which stem from human-induced modifications of the environment encompassing broad issues such as global climate change, alterations in land use, and the ingression of invasive alien species into their habitats. Invasive plant species are known for suppressing resident native plants (Pyšek et al. 2012). Responses of closely related invasive and native species to environmental factors were experimentally explored with respect to, e.g., soil nutrients (Powell and Knight 2009) or light and moisture (Skálová et al. 2013). However, studies on plant growth and reproduction in natural populations across variable habitat conditions are still limited, particularly those conducted on an appropriate scale. As established by Bell and Lachowicz (1991), environmental variance for traits related to reproductive success exists at scales relevant to plant growth and seed dispersal, including distances as small as 0.1–1.0 metres. Even at such a microhabitat scale, invasive species may be successful on account of significant environmental influences shaping key aspects of the species' ecology and facilitating their colonisation of new areas. Moreover, the considerable phenotypic plasticity of invasive species allows them to be flexible in their adaptation to varying environmental conditions (Sultan 1987; Parker et al. 2003; Berg and Ellers 2010). Such a small scale used in our research made it possible to describe in detail the microhabitat conditions of the species studied and resulted in an exceptionally high explanatory power (71–86%) of our multidimensional models, uncommon in ecological studies.

Intraspecific and interspecific habitat variations in the studied *Impatiens*

Research on distribution patterns of invasive species and attributes of their habitats offers valuable insights into their habitat preferences and the influence of environmental factors on their occurrence (Maron et al. 2004). Our studies comparing the habitat conditions of the native *Impatiens noli-tangere* with the alien invasive *I. capensis* revealed a broad spectrum of environmental settings in which the two species occurred. These environments range from heavily shaded, minimally disturbed forest habitats to open areas experiencing significant human impact. Although the distributions of the two species overlap to a large degree, the range of habitats supporting *I. noli-tangere* is narrower than that of *I. capensis*. This pertains to soil parameters (such as pH, organic matter content, and available forms of potassium, magnesium, silicon, sodium, manganese, zinc, lead, and nickel) as well as to the degree of shading and anthropogenic pressure. A detailed analysis of the *I. noli-tangere* habitat conditions showed the species to occur at forested sites, both heavily and lightly shaded, experiencing low and moderate levels of anthropogenic pressure. This suggests that native species may be more vulnerable to anthropogenic pressure which could potentially impact their distribution and population dynamics. Natural disturbances that result in partial opening of the tree canopy and improve light conditions are beneficial for the species. Under partially shaded conditions, *I. noli-tangere* individuals grow taller, and their flowering and fruiting are enhanced. Similar conclusions were drawn by Falińska (1979) and Hatcher (2003). In contrast, *I. capensis* is, in the area we studied, found predominantly in open, unshaded or partly shaded habitats subjected to moderate or even intense anthropogenic pressure. Our findings are consistent with those reported by other authors, e.g., Liendo et al. (2016), Myśliwy (2019), and Korpelainen and Pietiläinen (2023), who demonstrated that invasive species prefer anthropogenically disturbed habitats. In the next stage of invasion, the non-native species may spread into forest habitats, especially considering that *I. capensis* is an understory species in its native range. A similar pattern has already been observed with another species that shares comparable habitat preferences, *I. glandulifera*, which has started colonizing forested areas in recent years (Čuda et al. 2020). This suggests that *I. capensis* could follow a similar trend, posing a potential threat to the native *Impatiens* species. In our study, one site of orange balsam was located within a dense forest, characterised by heavy shading and minimal anthropogenic pressure. Importantly, individuals of *I. capensis* from the heavily shaded site did not differ significantly in their height and reproductive efficiency from those growing at more open sites. This suggests that *I. capensis* is highly tolerant to various levels of environmental disturbance and demonstrates its capability to colonize a wide range of habitats, including diverse light conditions. Moreover, the diverse physicochemical properties of soils at the study sites indicate that *I. capensis* has a pronounced ability to adapt to various soil conditions, which likely contributes to its successful colonization of new habitats. This is in agreement with conclusions drawn by Skálová et al. (2012) for the genus *Impatiens* and with the more general findings by Daehler (2003) who demonstrated the success of invasion and competition outcomes to depend on the ability to thrive under diverse environmental conditions. In its native range, *I. capensis* also occupies diverse environments with varying soil organic matter contents and insolation regimes (Lachowicz et al. 1988).

Factors underlying variation in growth and reproduction of studied *Impatiens*

The capacity of natural plant populations to sustain high reproductive success despite ongoing habitat changes, including those caused by humans, is essential for long-term survival of the populations. As we have shown, contrasting patterns in traits of the two *Impatiens* species stem from differences in responses to environmental factors. Our study suggests that *I. noli-tangere* is considerably more sensitive to the soil Pb content than *I. capensis*. In the multivariate analysis, lead was found to be the most critical factor determining the variability in trait composition of the native *Impatiens*, being negatively correlated with all growth and reproductive traits considered. In linear correlation analyses, nickel and zinc were also important elements, with their soil contents inversely proportional to most traits of *I. noli-tangere*. For *I. capensis*, the soil contents of lead, nickel, and zinc were not negatively correlated with traits related to growth and reproduction; on the contrary, the number of branches of the main stem correlated positively with these elements. The only exceptions were the sizes of leaves No. 2 and 3, which were inversely proportional to contents of the elements mentioned. In the *I. capensis* native range, an increased availability of potassium enhances all aspects of the species' growth and fecundity. Moreover, a higher soil organic matter content is also associated with an improved performance of the species (Lachowicz et al. 1988). As revealed by our research, significant, moderate, and positive correlations between the soil potassium and organic matter contents concerned only the number of stem branches in the invasive species. In contrast, the two factors exhibited moderate to strong inverse correlations with most traits of *I. noli-tangere*. Since the availability of elements in the soil changes with its pH, soil acidity is typically an important environmental factor affecting plant development (e.g. Więcław and Podlasiński 2013). For *I. capensis*, the literature contains inconsistent findings: while Waller (1980) suggested that reduced pH affects *I. capensis* growth, Simpson et al. (1985) did not observe such an effect. Our results confirm the importance of the soil pH. In both multivariate analyses and simple correlations, the soil pH was directly proportional to the plant size and the number of flowers in both species studied. However, for *I. capensis*, we observed moderate negative correlations between pH and leaf size. Moreover, there were significant negative correlations between the size of the leaves No. 2 and 3 (i.e., mature leaves) of the invasive species and the content of several soil elements (notably P, Si, Cr, Na, Fe, Mn, Cu, Ti, as well as the above-mentioned Pb and Zn). The soil calcium content, on the contrary, showed positive correlations with plant size of the two species.

In multivariate analyses, the degree of anthropogenic pressure emerged as a significant environmental variable, both in the analysis considering the two *Impatiens* species and in the analysis specific to *I. capensis*, consistent with findings in other species where habitat disturbance also plays a key role in shaping species traits (e.g. Więcław 2017). Our research demonstrated that increased anthropogenic pressure correlated with larger plant size of *I. capensis*. Such a relationship has previously been revealed in the species with respect to the seed size (Rewicz et al. 2020). It is important to note that the significance of increased anthropogenic pressure is related to the so-called co-occurrence of phenomena: the anthropogenically transformed habitats in our study are both deforested areas, characterized by the highest sunlight exposure (an important environmental factor in itself), and

areas subjected to various anthropogenic uses, which likely results in higher levels of soil contamination (e.g., with lead, zinc and nickel). The multivariate analysis showed the degree of shading to be the most influential factor in determining trait composition of *I. capensis*. Shading negatively affected the stem size but positively influenced the leaf size, likely due to the increase in leaf surface area compensating for poorer light conditions. This response of the increasing leaf length and width along an increasing shading gradient was not observed in the native species; quite the opposite, in *I. noli-tangere*, the simple linear correlation between the degree of shading and the leaf size was strong but inversely proportional. More importantly, the native *Impatiens* growing in heavily shaded areas produced fewer flowers and fruits, with a strong simple correlation between these traits and the degree of shading. In contrast, *I. capensis* showed no statistically significant correlation between shading and the number of fruits, while only a moderately inverse correlation was observed with the number of flowers. According to Simpson et al. (1985), light availability is the most important, and indeed the only environmental factor positively correlated with the observed growth differences in *I. capensis* individuals from different populations, in contrast to the soil moisture and nutrients (N, P, organic matter). Our results indicate that there are several significant environmental factors, not just the availability of light. This may have resulted from the appropriate scale used in studying ecological conditions of microhabitats, including the collection of separate soil samples for each *Impatiens* individual/specimen examined. Such studies are worth continuing, particularly when addressing bioindication of habitat conditions, including soil contamination.

In general, *I. noli-tangere* displays a higher intraspecific variability in growth and reproduction, with significantly higher coefficients of variation for all examined traits compared to *I. capensis*. This is supported by experimental findings reported by Skálová et al. (2012) who observed a higher plasticity in *I. noli-tangere*, compared to *I. capensis*. Particularly noteworthy is the variability in traits associated with reproductive success, such as the number of flowers and fruits. This higher variability, despite a narrower range of habitat conditions, may indicate a greater susceptibility to environmental changes or an increased risk of exposure to unfavourable conditions. This suggests that *I. noli-tangere* could be more sensitive to environmental changes or more vulnerable to local threats. Further research is needed to examine the impact of natural enemies of *Impatiens*, such as aphids, which are the dominant group among invertebrate pests (Najberek et al. 2017) and which, as revealed by our studies, more frequently attacked *I. noli-tangere* individuals. While these natural enemies emerged as a statistically significant factor in multivariate analyses addressing the variability in *I. capensis* traits, most simple correlations were not significant. Leaf damage caused by fungi had a more pronounced impact on the performance of the plants studied. Significant inverse moderate correlations were found between fungal damage and the stem height, flower and fruit numbers and leaf size of *I. noli-tangere*, whereas most traits of *I. capensis* did not show any significant associations with fungi. This supports the findings of Najberek et al. (2017) indicating that this type of stress does not significantly impact the overall invasiveness of *Impatiens* species. They concluded then that the resistance to pathogen enemies may have been established long before these plants were introduced to Europe.

Specific local conditions significantly influence the growth and reproduction of the plants studied, underscoring the importance of including species traits and local habitat conditions in addressing ecological questions and those aimed at understanding

species biology. This aligns with the findings of Dostál (2023) who demonstrated, using meadow species, that both fitness-related traits and niche differences are crucial for explaining plant responses to environmental changes. According to the modern coexistence theory framework (Chesson 2000), when one species exhibits higher growth and reproductive success, it is likely to outcompete another if niche differences between them are insufficient. Our study revealed a clear similarity in the ecological niches of the studied species. If the two species eventually come into contact, the lower performance of the native *I. noli-tangere* in natural populations could make it more vulnerable to population decline, potentially leading to its displacement by *I. capensis*. The displacement of native species by invasive ones, particularly among closely related species occupying similar ecological niches, has been well-documented (Dayan and Simberloff 2005; Čuda et al. 2015; Jauni and Ramula 2015).

Conclusions

The native European *Impatiens noli-tangere* and the invasive alien species *I. capensis* have overlapping habitat distributions, but the former occurs within a narrower range of environmental variables. Moreover, specimens of *I. noli-tangere* with the highest growth and reproductive performance were observed in semi-open, slightly shaded habitats, also preferred by *I. capensis*. The main environmental factors associated with intraspecific variation in growth and reproduction differ between the two *Impatiens* species, reflecting their distinct responses to environmental conditions. Contrasting effects on both species' traits were revealed in the degree of shading, soil pH, organic matter content, and several soil elements (e.g., P, K, Fe, Cu), including those indicating contamination (e.g., Pb, Zn, Ni). The high explanatory power of our models highlights the important role of microhabitat studies, at species-appropriate spatial scales, in invasion ecology. Our results show that there are no strong habitat barriers preventing the alien *I. capensis* from potentially expanding into areas occupied by the native *I. noli-tangere*. Currently, *I. capensis* invasion in Poland is in its early stages, and there have been no reports of both species co-occurring in European forests. However, given that *I. capensis* typically grows in the understory in its native range, it is possible that in the future, it could spread into forest habitats. The observed higher sensitivity of *I. noli-tangere* to environmental changes, along with its generally lower growth and reproductive output, raises questions about its potential vulnerability should *I. capensis* continue to spread. Further research is needed to assess the outcomes of their potential coexistence and interactions.

Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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Supplementary material 1

Additional information

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Data type: docx

Explanation note: **table S1.** Habitat conditions of individual locations of the studied *Impatiens* species (Int, *I. noli-tangere*; Ic, *I. capensis*) – basic statistical characteristics. **table S2.** The significance of differences in habitat parameters as well as presence or absence of aphid feeding and fungi damage between individual sites of native *I. noli-tangere* (Int) and invasive *I. capensis* (Ic) examined using the Kruskal-Wallis test and median test, with post hoc comparisons of the mean ranks of all pairs of sites (p value is given). **table S3.** The significance of differences in habitat parameters as well as presence or absence of aphid feeding and fungi damage between two *Impatiens* species: native *I. noli-tangere* (Int) and invasive *I. capensis* (Ic) examined using the Mann-Whitney U test with continuity correction. Results highlighted in red are statistically significant at $p < 0.05$. **table S4.** Basic statistical characteristics of growth and reproduction traits of the studied *Impatiens* populations (Int, *I. noli-tangere*; Ic, *I. capensis*). The lowest and highest average values have been bolded. Full names of the sites are given in table S1. **table S5.** The significance of differences in growth and reproduction traits between individual sites of native *I. noli-tangere* examined using the Kruskal-Wallis test and median test, with post hoc comparisons of the mean ranks of all pairs of sites (p value is given). Results highlighted in red are statistically significant at $p < 0.05$. **table S6.** The significance of differences in growth and reproduction traits between individual sites of invasive *I. capensis* examined using the Kruskal-Wallis test and median test, with post hoc comparisons of the mean ranks of all pairs of sites (p value is given). Results highlighted in red are statistically significant at $p < 0.05$. **table S7.** RDA summary for traits of studied *Impatiens* specimens (Int + Ic) and 19 environmental variables, as well as for *Impatiens noli-tangere* (Int) traits and 16 environmental variables, and *Impatiens capensis* (Ic) traits and 21 environmental variables, separately. **table S8.** Results of Spearman rank correlation between *Impatiens noli-tangere* traits and environmental variables. **table S9.** Results of Spearman rank correlation between *Impatiens capensis* traits and environmental variables.

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